# Multiple routes to interspecific territoriality in sister species of North American perching birds

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## ABSTRACT

Behavioral interference between species can influence a wide range of ecological and evolutionary processes. Here we test foundational hypotheses regarding the origins and maintenance of interspecific territoriality, and evaluate the role of interspecific territoriality and hybridization in shaping species distributions and transitions from parapatry to sympatry in sister species of North American perching birds (Passeriformes). We find that interspecific territoriality is pervasive among sympatric sister species pairs, and that interspecifically territorial species pairs

have diverged more recently than sympatric non-interspecifically territorial pairs. None of the foundational hypotheses alone explains the observed patterns of interspecific territoriality, but our results support the idea that some cases of interspecific territoriality arise from misdirected intraspecific aggression while others are evolved responses to resource competition. The combination of interspecific territoriality and hybridization appears to be an unstable state associated with parapatry, while species that are interspecifically territorial and do not hybridize are able to achieve extensive fine- and coarse-scale breeding range overlap. In sum, these results suggest that interspecific territoriality has multiple origins and impacts coexistence at multiple spatial scales.

**Keywords:** interspecific territoriality; interference competition; misdirected aggression; resource competition; passerine birds; sympatry

## INTRODUCTION

Behavioral interference between species, such as interspecific courtship, mate guarding and territorial defense, can have considerable impacts on the ecology and evolution of co-occurring species (Robinson and Terborgh 1995; Amarasekare 2002; Gröning and Hochkirch 2008; Grether et al. 2009, 2013; Kishi and Nakazawa 2013; Drury et al. 2015). The causes of different types of behavioral interference, their impacts on species coexistence, and the timescale over which they operate are active areas of research (Laiolo 2013; Martin and Ghalambor 2014; Losin et al. 2016; Grether et al. 2017; Kyogoku and Sota 2017; Sottas et al. 2018). Recent empirical and theoretical work has documented influences of interspecific territoriality on species coexistence and evolution in diverse taxa (reviewed in Grether et al. 2017). Interspecific territoriality has been shown to drive species replacements (e.g., Duckworth and Badyaev 2007) and to accelerate competitive exclusion (e.g., Pasch et al. 2013), but it also appears to stabilize coexistence between resource competitors in some cases (e.g., Ovadia and Dohna 2003; Ziv and Kotler 2003). While these recent findings highlight an important role for interspecific territoriality in ecological and evolutionary processes, it is difficult to predict just how interspecific territoriality influences the dynamics of interacting species. Part of the challenge is that a general explanation for the causes of interspecific territoriality remains elusive.

In theory, interspecific territoriality could evolve de novo between competing species for essentially the same reasons as intraspecific territoriality, but it also could arise as a byproduct of intraspecific territoriality when formerly allopatric species with similar territorial signals first come into contact. Regardless of how interspecific territoriality originates, selection in the zone of sympatry should strengthen adaptive responses to heterospecifics and eliminate maladaptive responses. Foundational hypotheses for the origin and persistence of interspecific territoriality posit that it is either an adaptive response to competition (see the resource competition, asymmetric competition, and reproductive interference hypotheses below) or a maladaptive byproduct of intraspecific territoriality (the misdirected aggression hypothesis).

Under the resource competition hypothesis, interspecific territoriality evolves or persists between species with substantial niche overlap because territory holders benefit from the reduction in exploitative resource competition (Orians & Willson 1964; Cody 1969, 1973; Grether et al. 2009). In other words, under this hypothesis, interspecific territoriality is a mechanism of spatial resource partitioning that benefits dominant individuals of both species (Cody 1969, 1973; Grether et al.

2009). One variant of this hypothesis additionally predicts that interspecific territoriality should primarily be seen in structurally simple habitats (e.g., grassland) where the species are unable to diverge sufficiently in resource use to make interspecific territory defense unprofitable (Orians and Willson 1964). The asymmetric competition hypothesis also assumes strong resource competition but is based on the premise that only dominant individuals of dominant species benefit from interspecific aggression (MacArthur 1972). Thus, this hypothesis predicts that interspecific territoriality is more likely to occur when one species is behaviorally dominant over the other.

While these first two hypotheses consider interspecific territoriality to be a consequence of resource competition, interspecific territoriality may also benefit species that engage in reproductive interference, such as hybridization. The reproductive interference hypothesis posits that interspecific territoriality can evolve or be maintained by selection arising from local mate competition between species that are incompletely reproductively isolated (e.g., due to indiscriminate male mate recognition; Payne 1980; Drury et al. 2015). This hypothesis has mainly been invoked to explain interspecific territoriality between species that are not resource competitors (Payne 1980; Drury et al. 2015), but mate defense and resource defense are both functions of intraspecific territoriality and the same might be true for some cases of interspecific territoriality.

Finally, interspecific territoriality may not serve an adaptive purpose and instead have a net cost for both species. The misdirected aggression hypothesis assumes that interspecific territoriality arises as a byproduct of intraspecific territoriality and lowers the fitness of the aggressors (Orians & Willson 1964; Murray 1971). Such maladaptive behavior would not be expected to persist indefinitely. However, maladaptive interspecific territoriality may be observed if species have only recently come into contact or usually occupy different habitats and thus encounter each other infrequently (i.e., low syntopy; Losin et al. 2016).

Determining which of these hypotheses explain(s) interspecific territoriality is important for building a general understanding of how interspecific territoriality affects the local coexistence and evolutionary dynamics of interacting species. Whether interspecific territoriality generally hinders or stabilizes local coexistence may also translate to patterns at broader geographic scales, such as the ability of species to co-occur in extensive sympatry. Previous studies on species interactions provide reasons to expect that interspecific territoriality could impact whether species are sympatric. Interspecific territoriality has been shown to impact range limits along elevational gradients (Jankowski et al. 2010; Pasch et al. 2013; Freeman et al. 2019). Additionally, other types of interactions between competitors, such as resource competition and hybridization, have been shown to constrain how quickly sister species across vertebrate groups become sympatric after allopatric speciation (Price 2010; Weir and Price 2011; Pigot and Tobias 2013; Laiolo et al. 2017).

Whether interspecific territoriality is primarily maladaptive or adaptive leads to different expectations for how it impacts sympatry. If interspecific territoriality is a maladaptive byproduct of misdirected intraspecific aggression, it could reduce the rate at which parapatric species expand their ranges into broadly overlapping sympatry. This prediction is consistent with how resource competition and hybridization are thought to impact species range overlap. Alternatively, if interspecific territoriality stabilizes the local coexistence of closely related species, strong resource competitors, and/or hybridizing species, it could allow these species to transition more rapidly into sympatry than if they were not interspecifically territorial. For example, two allopatric species with extensive resource overlap could expand into sympatry without diverging in resource use if engaging

in interspecific territoriality allows them to spatially partition the limiting resource (Grether et al. 2013).

Although the foundational hypotheses for interspecific territoriality were inspired by observations in particular species pairs, developing a general understanding of the origins and maintenance of this behavior requires a comprehensive study across a broad taxonomic group. The wealth of information available on North American birds, including a long record of behavioral observations and species occurrences, makes this an ideal system for testing hypotheses about interspecific territoriality. We compiled field observations of interspecific territoriality and a variety of ecomorphological traits for the largest order of North American birds (Passeriformes). In Drury et al. (2020), we present a comparative analysis of territoriality between species pairs across the entire clade. That analysis shows that resource competition and reproductive interference are the primary evolutionary drivers of interspecific territoriality in passerine birds. Because that analysis includes many distantly related species pairs that have likely interacted for millions of years (average divergence time = 30.9 Ma), however, its results best characterize the persistence of interspecific territoriality over long timescales. What remain unclear are the origins of interspecific territoriality, including whether it can emerge as a maladaptive phenomenon. Addressing this question requires studying the drivers of interspecific territoriality among the most recently diverged species pairs.

In this paper, we present a sister taxon-based analysis in which only the youngest interspecifically territorial species pairs of North American passerine birds are compared to non-interspecifically territorial sister species pairs. Focusing on the youngest sympatric species pairs in the clade allows us to characterize how interspecific territoriality affects the dynamics of relatively recent species interactions, and therefore increases the likelihood of detecting patterns predicted by the misdirected aggression hypothesis. Considering that interspecific territoriality could arise and persist for different reasons in different species pairs, we deduced and tested for patterns predicted by the misdirected aggression hypothesis and each of the other hypotheses in combination (Figure 1). Finally, we use the sister taxa data to test for effects of interspecific territoriality on species coexistence in sympatry.

## METHODS

### Species pairs identification and classification

Our dataset consists of sister species of passerine birds that breed in North America and that overlap in breeding range. We identified sister species by sampling $10^4$ trees from the posterior distribution of a North American passerine phylogeny (Hackett et al. 2008; Jetz et al. 2012) and selecting those that appeared as sister species in 90% or more of the phylogenies. Since allopatric sister species do not have the opportunity to be interspecifically territorial, we excluded species pairs that are allopatric in the breeding season according to 2016 and 2017 species distribution shapefiles from BirdLife International (www.birdlife.org). For each allopatric sister species pair, we selected the next most closely related species in the phylogeny that is sympatric with only one of the allopatric species to form a pair of closely related sympatric species. We only did this for one species from each allopatric pair to avoid sampling from non-independent nodes. We then created a maximum clade credibility tree from this posterior distribution in TreeAnnotator v1.8.4 (Suchard et al. 2018). Next, we calculated patristic distance between species from this phylogeny using the cophenetic.phylo function in the R package ape (Paradis et al. 2004). Due to recent taxonomic splits,

we could not calculate patristic distance for all species pairs using this method. We obtained the patristic distance for one such pair, *Troglodytes pacificus* and *T. hiemalis*, from the literature (Toews and Irwin 2008). The other two species pairs that lacked patristic distances were omitted from our analyses.

We determined whether each species pair is interspecifically territorial with comprehensive literature searches using Web of Science, Birds of North America Online (Rodewald 2015), ProQuest Theses and Dissertations, and Google Scholar. We also contacted Birds of North America Online authors for additional behavioral observations. As in Losin et al. (2016), we considered a study sufficient evidence for interspecific territoriality if it contained at least two accounts of interspecific territorial aggression between unique individuals. Behaviors that qualified as interspecific territorial aggression include aggressive displays or countersinging, fighting, or chasing a heterospecific from a territory. We did not consider aggression over a food source or defense of a nest from a predator to be evidence of interspecific territoriality. Aggressive response to playbacks of territorial song and expansion of territory in response to removal of heterospecifics supported the classification of interspecific territoriality but were not required, since not all species pairs had been studied with these methods. If the behavior of both species in a pair had been studied together and no interspecific territoriality was reported, we classified that pair as non-interspecifically territorial. We omitted from our dataset any species pairs whose behavior had not been studied in sympatry (25 pairs), with two exceptions: the *Empidonax* species *E. difficilis* and *E. occidentalis* and the *Troglodytes* species *T. pacificus* and *T. hiemalis* have only recently been recognized as separate species (Johnson 1980; Toews and Irwin 2008), and have been reported to have non-overlapping territories in sympatry, so we classified them as interspecifically territorial. We also excluded species pairs for which neither species in the pair was intraspecifically territorial (2 species pairs), or for which we lacked data on fine-scale breeding habitat overlap (1 species pair). A full list of species pairs can be found in Table S1.

To determine whether species hybridize in the wild, we consulted McCarthy (2006) and searched the literature for newer reports of hybridization through 2018. We considered McCarthy's (2006) "Natural Hybridization Reported" category as sufficient evidence for hybridization, although several species pairs in our dataset have been reported to have ongoing or extensive hybridization. We did not consider weaker categories of evidence (McCarthy's "Hybridization Inferred" categories) or reports of hybridization in captivity to be sufficient evidence for classifying species as hybridizing in our analysis.

To assess whether greater study effort increased the likelihood of species pairs being reported as interspecifically territorial, we used the number of records of each species pair in the Zoological Records database (Thomson Reuters, New York, NY) as a proxy for past research effort and used Mann-Whitney tests to compare interspecifically versus non-interspecifically territorial species.

## Breeding range and habitat overlap quantification

We used two metrics to represent breeding season range overlap and habitat overlap of species pairs. First, we calculated the proportion of breeding range sympatry by dividing the area of overlap between BirdLife shapefiles by the breeding range area of the species with the smallest breeding range in each pair. However, BirdLife shapefiles were missing for two species pairs. We therefore also estimated sympatry using the Breeding Bird Survey (BBS; Sauer et al. 2017), a dataset

of transects run across North America during the breeding season since the 1960s to survey the number of birds observed. Each BBS route is run annually, with 50 stops along each route. We measured sympatry by dividing the number of routes shared by both species by the total number of routes where the species with the fewest routes was observed. To replace the missing Birdlife sympatry values with rescaled BBS sympatry estimates, we used predicted values from a zero-intercept linear regression of the available Birdlife sympatry estimates on the BBS sympatry estimates ($R^2$ = 0.69, df = 85, $P$ < 0.0001).

Our second measure of overlap was syntopy (Rivas 1964), a fine-scale measure of breeding habitat overlap within the region of sympatry, such that species with higher syntopy are more likely to occur in the same habitat at the same time within their breeding range. We measured syntopy by identifying BBS routes where both species in a breeding season were found and dividing the number of "shared" stops (where both species were observed) by the number of stops where either species was observed. For two sympatric species pairs without BBS data (*Plectrophenax hyperboreus* and *Plectrophenax nivalis*; *Ammodramus caudacutus* and *Ammodramus nelsoni*), we used rescaled measures of syntopy from eBird records (Sullivan et al. 2009) (Supplemental Analysis 1).

## Ecological trait quantification

To determine whether interspecific territoriality can be predicted by species-level traits, we collected ecomorphological data for each species and calculated the absolute value of the difference between these traits for each species pair. We focused on male traits since males perform territorial displays and defense for all territorial species in our dataset. We collected mass and bill length (exposed culmen length) values from the Birds of North America Online or additional references (e.g., Oberholser 1974, Dunning 2008). To account for possible geographic variation in the traits, when possible we used measurements collected close to the location where interspecific territoriality was studied. If the bill length measurement we found for a species was a measurement from the nostril to the tip of the bill instead of the exposed culmen length, we used a linear regression equation based on species for which both types of measurements were available ($R^2$ = 0.985, df = 23, $P$ < 0.0001) to predict exposed culmen length from the nostril-to-tip measurement.

We categorized foraging guild overlap between species in a pair by calculating the number of foraging guild axes on which the species overlap based on de Graaf et al. (1985). Specifically, species were categorized by the food types, foraging techniques, and foraging substrates used during the breeding season, and each species pair was assigned a score (1 or 0) based on whether or not they overlap in all three axes.

We categorized the habitat complexity of each species using descriptions from the Birds of North America Online and categories from Losin et al. (2016), with 1 representing a simple habitat such as a grassland, marsh, or tundra, 2 representing intermediate habitat, such as chaparral or forest edge, and 3 representing complex habitat such as deciduous forest.

## Quantification of territorial signal similarity

To determine whether interspecific territoriality could be predicted by overlap in common territorial signals, we quantified species similarity in territorial song and plumage coloration. To assess similarity in song, we downloaded high quality sound files from xeno-canto (https://www.xeno-canto.org/) and the Cornell Macaulay Library (Table S2) that matched the description in the Birds of North America of the vocalization used by each species for territorial

advertisement and interactions. We categorized the size of the territorial repertoire for each species with descriptions in the Birds of North America, and determined the number of song files needed to capture repertoires of different sizes with a sensitivity analysis (Supplemental Analysis 2, Figure S1). For species with relatively small repertoires (fewer than 4 song types), we collected 2 representative song files, and for species with relatively large repertoires (4 or more song types), we collected 4 song files. We performed noise reduction on sound files with background noise in Audacity version 2.1.3 (http://web.audacityteam.org/), using starting values of noise reduction = 12, sensitivity = 6, frequency smoothing = 0. We then used the Audacity normalize function to standardize the amplitudes of all sound files.

To assess similarity in song between the species in a pair, we used two approaches. First, we calculated a measure of song dissimilarity based on numerous song parameters. We used the R package warbleR (Araya-Salas and Smith-Vidaurre 2016) to extract acoustic parameters (Table S3) and then additionally calculated the number of notes, length of the longest note, total note duration, average note duration, longest pause between notes, and average pause length per song. We averaged parameters for the sound files for each species and performed principal component analysis (PCA; Figure S2) on these averaged parameters. We then calculated the Euclidean distance between all principal component scores for each species pair as a measure of song dissimilarity.

Second, we used spectral cross-correlation analysis (Clark et al. 1987) to quantify similarity in the frequency-time structure of song files. Spectral cross-correlation incrementally time-shifts spectrograms and calculates the cross-correlation between the frequency-time matrices of the spectrograms at each increment. We used the xcor function in warbleR to perform spectral cross-correlation analysis between all song files in a species pair, and averaged the maximum cross-correlation value from those comparisons as a second metric of song similarity. These two song measures are correlated ($r$ = -0.37, $N$ = 45, $P$ = 0.011), but are not redundant/collinear ($VIF_{PCA}$ range = 1.16 – 1.93, $VIF_{cross\text{-}correlation}$ range = 1.65 – 2.02 across all models).

To quantify similarity in plumage coloration and pattern, we recruited volunteers to score images of birds based on how dissimilar they appeared. We obtained digital images of each species from two field guides (Sibley 2000; Dunn and Alderfer 2006) and asked participants to rank the plumage dissimilarity of each species pair on a 0-4 scale using those images. We partitioned the images into seven comparison sets that we distributed with Survey Gizmo (https://www.surveygizmo.com) through social media and birding groups. Each comparison set started with a training set of 4 species pairs to help acquaint volunteers with the dissimilarity scale and then presented a series of approximately 30 pairs of images, with images repeated across and within comparison sets, and a test for colorblindness. We filtered out incomplete responses and responses from participants who failed the color vision test. After obtaining at least 10 complete responses per comparison set, we calculated the mean dissimilarity score for each species pair. Plumage dissimilarity scores were strongly correlated between field guides (Spearman correlation $\rho$ = 0.79, $N$ = 14), within comparison sets ($\rho$ = 0.92, $N$ = 14), across comparison sets ($\rho$ = 0.85, $N$ = 14), and with a plumage distance metric based on spectrally calibrated photos of bird specimens and an avian color vision model ($\rho$ = 0.73, $n$ = 104; Supplemental Analysis 3; Figure S3)

## Assessing ecological predictors of interspecific territoriality

We first used univariate tests to determine whether the trait differences (such as song similarity or bill length difference) within interspecifically territorial species pairs differed from non-

interspecifically territorial species pairs. Because the potential to detect such differences depends on the level of variability among sister species, we calculated coefficients of variation for traits measured on a ratio scale and coefficients of nominal variation for binary traits (Kvålseth 1995).

To assess whether a single hypothesis explained the observed pattern of interspecific territoriality, we ran a generalized linear model with interspecific territoriality as a binomial response variable and the ecological, phenotypic, and behavioral traits in Table 1 as the predictor variables: hybridization (presence or absence), overlap in all three foraging niche axes (yes or no), and six continuous variables: syntopy, ecomorphological differences (mass and bill length), song similarity (PCA distance and maximum spectral cross-correlation), and plumage similarity.

To test the hypothesis that interspecific territoriality persists among ecological competitors living in simple habitats (Orians and Willson 1964), we performed a Fisher's exact test to evaluate whether interspecific territoriality depends on the complexity of the habitat.

To determine if interspecific territoriality arises in diverse ecological circumstances, we examined whether multiple hypotheses explain the occurrence of interspecific territoriality in the species pairs. To do this, we added to the generalized linear model interactions between syntopy and variables that are proxies for resource or mate competition based on the following logic: maladaptive interspecific territoriality, arising from misdirected aggression, should not persist between species that overlap extensively in breeding habitat and encounter each other frequently, whereas interspecific territoriality that is adaptive because it enables coexistence between competitors could persist between such species (Figure 1A; Losin et al. 2016). Thus, the presence of species that engage in interspecific territoriality, are strong competitors, and are highly syntopic supports the view that interspecific territoriality is adaptive, and interspecific territoriality that is associated with low levels of syntopy supports the view that this behavior is maladaptive (Figure 1).

To evaluate whether the misdirected aggression hypothesis and the reproductive interference hypothesis each explain a subset of the cases of interspecific territoriality, we included an interaction term between syntopy and hybridization. Under these two hypotheses, interspecific territoriality should primarily occur between non-hybridizing species with infrequent encounters or between hybridizing species that encounter each other frequently (Figure 1B). To test whether the misdirected aggression hypothesis and the resource competition hypothesis each explain a subset of the cases of interspecific territoriality, we included an interaction term between syntopy and the number of overlapping foraging guild axes. Under these two hypotheses, interspecific territoriality should primarily occur between species that encounter each other infrequently or between species with very similar ecological niches and breeding habitats (Figure 1C). Size asymmetry could be a proxy for exploitative resource competition (Losin et al. 2016), but also for whether one species is likely to dominate the other in aggressive interactions (Martin and Ghalambor 2014; Martin et al. 2017; Miller et al. 2017; Chock et al. 2018). Since sister species are on average very phenotypically similar, mass difference may not be a strong proxy for species differences in niche overlap, but even a small difference in size could impact aggressive interactions. Thus, we assume that size asymmetry is a better proxy for asymmetry in aggressive dominance than for resource competition in our dataset, and include an interaction term between syntopy and mass difference to test whether the misdirected aggression and asymmetric competition hypotheses each explain a subset of the cases of interspecific territoriality. Under these two hypotheses, interspecific territoriality should primarily occur between species that encounter each other infrequently or that occupy the same breeding habitats and are asymmetric in size (Figure 1D). While it is possible that there could be additional or

more complex interactions that describe the occurrence of interspecific territoriality in these species, we selected these interactions based on our hypothesis framework.

For each of these linear models, we ran a second generalized linear model that included patristic distance as a predictor variable to control for differences in time since species diverged.

## Modeling transitions to sympatry

We used two approaches to test whether interspecific territoriality or the combination of interspecific territoriality and hybridization affects the degree to which species pairs are sympatric. The first approach assessed the effect of these behaviors on the percent of breeding range overlap using generalized linear models. The second discretized the percent of breeding range overlap into the categories of parapatry and sympatry, and estimated the probability of species pairs transitioning from parapatry to sympatry.

In the first approach, we examined whether interspecific territoriality impacts sympatry using two generalized linear models with percent breeding range overlap as the response variable (using the R package betareg; Cribari-Neto and Zeileis 2010). The first model included interspecific territoriality, hybridization, and patristic distance as predictors to examine the effect of interspecific territoriality on sympatry while controlling for hybridization and divergence time, since extensive overlap in sympatry is positively associated with divergence time and the degree of reproductive isolation in other sister taxa (Weir and Price 2011; Pigot and Tobias 2013; Laiolo et al. 2017). In the second model, we added an interaction term between interspecific territoriality and hybridization to assess whether the effect of interspecific territoriality on the amount of sympatry depends on whether species hybridize. If interspecific territoriality is an overall costly behavior, the combination of hybridization and interspecific territoriality could hinder species' ability to co-occur in extensive sympatry. If instead interspecific territoriality is an adaptive response to reproductive interference, it might enable hybridizing species to achieve broader sympatry than if they did not engage in interspecific territoriality.

We complemented this approach by also constructing two sets of models based on Shi et al. 2018 to estimate the probability of sister species transitioning from parapatry to sympatry. The first set of models assumes that the probability of achieving sympatry is affected by our covariates (either interspecific territoriality or the combination of interspecific territoriality and hybridization), but not divergence time. The second set of models assumes that divergence time does impact the probability of sympatry, with this effect potentially differing by the covariate. These models assume allopatric speciation, which is thought to be the predominant mode of speciation in birds (Mayr 1942; Coyne and Orr 2004; Phillimore et al. 2008), and that following speciation, species transition from allopatry to parapatry before coming into broadly overlapping secondary sympatry (Cooney et al. 2017). Because these models require species pairs to be classified as either parapatric or sympatric, we tested a range of values of percent breeding range overlap (in 5% increments between 20% and 65%) to serve as a cutoff value between parapatric and sympatric distributions, as in Cooney et al. (2017). We only considered transitions from parapatry to sympatry and not from allopatry to sympatry because it is not possible for allopatric species pairs to exhibit behavioral interference.

Finally, since the range of divergence times in a dataset can impact the generalization of how divergence time relates to sympatry from that dataset to other systems, we examined the range of phylogenetic distances in our dataset relative to other studies of sympatry in avian sister

species (Supplemental Analysis 5). To determine whether the species pairs in our dataset are older than average passerine sister species, we compared the phylogenetic distances between species pairs in our dataset to those of randomly sampled passerine sister species pairs (Supplemental Analysis 5, Figure S4).

All data processing and statistical analyses were performed in R version 3.5.0 (R Core Team 2019). All data and code to recreate analyses are deposited in the Dryad Digital Repository: https://doi.org/10.5068/D11T2D (Cowen et al. 2020).

## RESULTS

### Data Summary

In our dataset of true North American passerine sister species ($n$ = 75 pairs), 63 (84%) pairs overlap in breeding range, with average range overlap of 44.2% of the range of the species with the smaller range. Of those, 35 (56%) are sympatric, defined as having at least 20% breeding range overlap. Only 12 sister species pairs are allopatric, and the remaining 28 are parapatric (< 20% breeding range overlap). After replacing allopatric sister species with the most closely related sympatric or parapatric species pairs, we were left with 71 phylogenetically independent pairs of closely related species. We were able to classify 48 of the 71 species pairs as interspecifically territorial or not. Excluding species that lacked information on patristic distance or breeding range overlap, our final dataset consisted of 45 sympatric or parapatric species pairs. Of those, 21 pairs (47%) are interspecifically territorial.

In general, the species pairs in our dataset have similar plumage and song and overlap greatly in foraging guild, and also have low coefficients of variation for these variables (Table 2; coefficient of nominal variation for foraging guild overlap = 0.53, with 73% of species pairs overlapping in all axes). The paired species vary most in morphological trait differences, syntopy, and sympatry (Table 2), and are relatively evenly divided across the categories of interspecifically territorial/non-interspecifically territorial and hybridizing/non-hybridizing (coefficient of nominal variation = 0.93 and 0.8, respectively). The average divergence time between species pairs is 4.7 Ma (range = 0.4 Ma – 34 Ma; Figure 2).

To assess the likelihood of there being unreported cases of interspecific territoriality in our dataset, we examined whether study effort predicted the probability of species pairs being categorized as interspecifically territorial, and found that indeed it did. There were more records in the Zoological Records database for species pairs classified as interspecifically territorial than for species pairs classified as non-interspecifically territorial ($range_1$ = 0 – 53; $range_2$ = 3 – 105; $median_1$ = 7; $median_2$ = 15; Mann-Whitney test, $n_1$ = 24, $n_2$ = 21, $P$ = 0.015). This suggests that additional study of some of the species pairs currently classified as non-interspecifically territorial could uncover evidence that they do engage in interspecific territoriality.

### Ecological predictors of interspecific territoriality

Interspecifically territorial species pairs are more closely related than non-interspecifically territorial species pairs (Table 2; Figure 2), but species pairs in these two categories do not differ significantly in territorial signals, morphology, syntopy, sympatry (Table 2), hybridization (15 of 21 interspecifically territorial vs. 12 of 24 non-interspecifically territorial species pairs hybridize, Fisher's exact test, $P$ = 0.22), or foraging guild (15 of 21 interspecifically territorial vs. 18 of 24 non-interspecifically territorial species pairs overlap in all foraging axes, Fisher's exact test, $P$ = 1).

The generalized linear models without interaction terms that we used to assess support for the four hypotheses separately (Table 1) yielded no significant predictors of interspecific territoriality (Tables S4, S5). However, in models with an interaction between hybridization and syntopy, the interaction term was significant: among hybridizing species, interspecifically territorial species are less syntopic than non-interspecifically territorial species, whereas among non-hybridizing species, interspecifically territorial species are more syntopic than non-interspecifically territorial species (Figure 3A, Table 3, S6). The results for hybridizing species are consistent with the misdirected aggression hypothesis but not with the reproductive interference hypothesis (Table 1, Figure 1B), while the results for the non-hybridizing species are consistent with the resource competition or the asymmetric competition hypotheses (Figure 1C, 1D).

The models with an interaction between foraging guild overlap and syntopy yielded no significant terms (Tables S7, S8). In the models with an interaction between mass difference and syntopy, however, the interaction term emerged as positively associated with interspecific territoriality, regardless of phylogenetic correction, suggesting support for the misdirected aggression and the asymmetric competition hypotheses (Figure 3B, Tables 4, S9).

In contrast to Orians and Willson's (1964) prediction, habitat complexity did not differ between interspecifically territorial and non-interspecifically territorial species pairs (Fisher's exact test, $P = 0.17$), with most interspecifically territorial species pairs (32 out of 42 pairs we could score) occurring in complex or intermediate habitats.

### Transitions to sympatry

The regression models we used to examine whether interspecific territoriality impacts the extent of breeding range sympatry suggested that the interaction of interspecific territoriality and hybridization may predict the percent of breeding range overlap; species that both are interspecifically territorial and hybridize appear to have narrower breeding range overlap relative to other species in the dataset, although this was not statistically significant ($P = 0.07$; Table S11; Figure 4). Interspecific territoriality on its own, controlling for hybridization and patristic distance, did not predict the degree of breeding range overlap, nor did patristic distance on its own (Table S11).

The approach we used to assess the probability of occurring in sympatry yielded similar results: the best model for describing the probability of sympatry included the interaction between interspecific territoriality and hybridization and did not include divergence time, regardless of the threshold of parapatry-sympatry considered (Tables S12-S18).

The true sister species pairs in our dataset are not significantly older than random samples of passerine sister species pairs worldwide (Figure S4; Supplemental Analysis 5).

## DISCUSSION

We found that interspecific territoriality occurs in almost half of all sympatric sister species of North American passerine birds. This finding alone suggests that interspecific interference competition ought to be an important consideration for researchers studying distributional patterns and diversification in birds. In this light, it is relevant to ask: is interspecific territoriality a maladaptive byproduct of intraspecific territoriality that reduces the prospects of species coexisting (Murray 1971) or instead is it an evolved (adaptive) mechanism of spatial resource partitioning that stabilizes coexistence (Grether et al. 2013)? Our results indicate that interspecific territoriality has

both maladaptive and adaptive origins, and has important consequences for whether species can be extensively sympatric.

Consistent with all four hypotheses (Table 1), we found that interspecifically territorial sister species are more closely related than non-interspecifically territorial sister species, despite the shallow timescale involved. Beyond that, however, none of the foundational hypotheses' specific predictions held up across the entire clade. Instead, we found evidence that multiple hypotheses together could explain the distribution of interspecific territoriality.

**Multiple origins of interspecific territoriality**

Our approach for evaluating support for multiple hypotheses (Figure 1) generated two key findings. First, we found that interspecifically territorial species pairs that are low in syntopy (i.e., overlap very little in habitat) are on average more similar in size than interspecifically territorial species pairs that frequently co-occur in the same habitat (Figure 3B). This result is consistent with the misdirected aggression and asymmetric competition hypotheses each explaining a subset of cases (Figure 1D). Support for these hypotheses implies that interspecific territoriality can arise between species that are phenotypically similar and rarely encounter each other, and can also arise between species that frequently encounter each other and compete for resources, especially when one of the species dominates and benefits from interspecific territorial interactions. This is the first evidence for either of these two hypotheses in a comparative study.

Our interpretation that relatively large differences in body mass among highly syntopic species support the asymmetric competition hypothesis assumes that body size asymmetries are proxies for asymmetries in aggressive dominance, an assumption that warrants further empirical study. While larger species indeed often dominate aggressive interactions between closely related species (Martin and Ghalambor 2014; Martin et al. 2017; Chock et al. 2018; Freeman 2019), we lacked sufficient data to verify whether this was true of the species pairs in our study (Supplemental Analysis 4). We encourage future field studies of interspecific territoriality to document which species instigate and/or dominate observed interspecific territorial interactions, as this would more clearly characterize the role of aggressive asymmetries in the origin and maintenance of interspecific territoriality. Such data could also be valuable for predicting evolutionary and ecological outcomes of interspecific interactions (e.g., Martin and Bonier 2018), just as asymmetries in exploitative competition or reproductive interference can impact species coexistence (Tilman 1980; Amarasekare 2002; Kishi and Nakazawa 2013).

Even if size difference in closely related North American passerines does not predict which species dominates territorial interactions, size could still play an important role in the emergence of interspecific territoriality as an adaptive response to resource competition. For example, large differences in size could indicate asymmetric efficiency at exploiting a common limiting resource (Persson 1985), and interspecific territoriality could provide enough of an advantage to the less efficient resource exploiter for the two species to coexist (Grether et al. 2013). Alternatively, our finding that highly syntopic pairs of interspecifically territorial species tend to be more dissimilar in size than less syntopic species could represent divergence in morphology driven by ecological character displacement.

The second key result from our study is that hybridizing species are more likely to be interspecifically territorial when they rarely encounter each other (Figure 3A). This does not support the hypothesis that interspecific territoriality is generally an adaptive response to reproductive interference among sister passerine birds. Instead, it suggests that many sister species engage in

high levels of behavioral interference (both interspecific territoriality and hybridization) that is overall costly and might eventually be eliminated by agonistic character displacement (Grether et al. 2017). The presence of non-hybridizing interspecifically territorial species that frequently co-occur in time and habitat, however, suggests that interspecific territoriality may also arise as an adaptive response to resource competition among species that overlap broadly in breeding habitat.

These two key findings together suggest that the combination of hybridization and interspecific territoriality in closely related species is an unstable state that only persists when species have low encounter rates, but that in the absence of hybridization, interspecific territoriality can mediate resource partitioning among highly syntopic species, especially when one species is much larger in body size than the other. This interpretation has an important caveat: if the misdirected aggression and resource competition hypotheses together accounted for the cases of interspecific territoriality we observed in sister passerine species, we would expect to see a positive interaction between foraging guild overlap and syntopy (Figure 1C), but we did not find such an association (Tables S7, S8). This might be due to low variation in the foraging guild metric, since most species pairs in our dataset overlapped in all three foraging guild axes. Moreover, foraging guild may be a poor predictor of actual resource competition between passerines, as recent work has shown that species in distinct foraging guilds can overlap substantially in resource use (Kent and Sherry 2020).

**Origins, persistence, and impacts of interspecific territoriality in context**

At the level of the entire clade of North American passerine birds, in a study that included territoriality between species from different genera and even different families, Drury et al. (2020) found clear evidence that interspecific territoriality is an adaptive response to resource competition and reproductive interference. In this paper, we focused on the youngest sympatric species in this clade, and found evidence that the asymmetric competition and the misdirected aggression hypotheses together explain the origins of interspecific territoriality.

That we found evidence for the misdirected aggression hypothesis while Drury et al. (2020) did not can be explained by the difference in divergence times considered in the two datasets (mean divergence time of the species pairs = 30.9 Ma in Drury et al. (2020) and 4.7 Ma in this paper). Although interspecific territoriality that originates as misdirected intraspecific aggression could occur in a dataset of mostly distantly related species, detecting it in a dataset of sister species is much more likely for two reasons. First, territoriality between species that arises due to misdirected aggression and is costly for both species is unlikely to persist over long evolutionary timescales as species interact frequently and evolve mechanisms to discriminate between conspecifics and heterospecifics (Figure 1A). Interspecific territoriality that does persist over long timescales is more likely to be adaptive for one or both species (Figure 1A). Second, species that come into contact after a long period of divergence in allopatry are unlikely to make mistakes in competitor recognition because territorial signals generally diverge over time. Thus, interspecific territoriality that arises after long divergence times would generally evolve de novo as an adaptive response to competition. By contrast, secondary contact between sister species could lead to misdirected aggression since these species are often quite similar phenotypically.

Having shown that interspecific territoriality is common among North American passerines, we asked how it affects breeding season sympatry to determine whether it shapes species coexistence at larger spatial scales. Our “transitions to sympatry” analysis reveals that while neither interspecific territoriality nor hybridization alone prevents extensive sympatry (Figure 4, Table S11),

the combination of these two forms of behavioral interference might prevent closely related species from becoming extensively sympatric. Furthermore, we did not find that divergence time predicts whether species are in sympatry (Table S11). This contrasts with patterns found in other avian groups of similar age (e.g., ovenbirds, Tobias et al. 2014; Old World warblers, Price 2010; Supplemental Analysis 5), but might be consistent with evidence that waiting times to sympatry are relatively short in temperate North America (Weir and Price 2011; Weir and Price 2019).

Taken together, our findings lend insight into the important role of interspecific territoriality in the early stages of secondary contact following allopatric speciation. Our results point to a possible stage in the speciation process of secondary contact between closely related species that treat each other as competitors and mates, thus remaining in parapatry until they diverge sufficiently in competitor and mate recognition. Other closely related species, however, have achieved breeding range sympatry and extensive fine-scale breeding range overlap along with, and perhaps in part because of, interspecific territoriality. We found that interspecific territoriality is common among closely related species of passerine birds, but that even at the tips of the phylogeny, the ecological circumstances associated with interspecific territoriality are diverse. Our work suggests that the evolutionary stability of interspecific territoriality may also vary across taxa, and calls for additional empirical research to further improve our understanding of how interspecific territoriality arises and contributes to the evolution and coexistence of animal species.

## Figures Captions and Tables

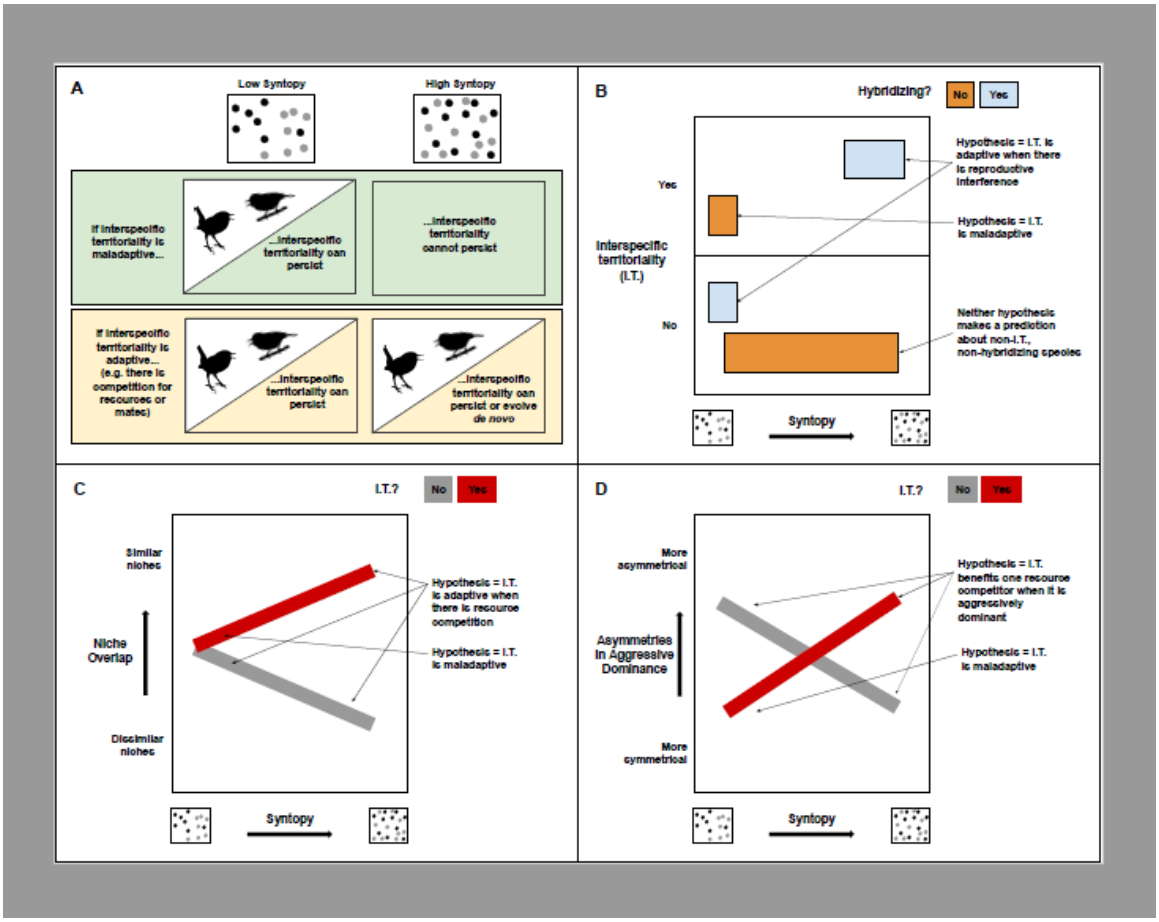

Figure 1. Predicted results if more than one hypothesis explains the pattern of interspecific territoriality observed across closely related species. Arrows identify outcomes consistent with a given hypothesis. (A) Whether maladaptive interspecific territoriality could persist depends on the degree of overlap in breeding habitat (i.e., syntopy). (B) If the misdirected aggression and reproductive interference hypotheses each account for a subset of cases of interspecific territoriality, interspecific territoriality should primarily be found between species that rarely encounter each other (low syntopy) or between hybridizing species that encounter each other frequently (high syntopy). The reproductive interference hypothesis further predicts that hybridization hinders extensive co-occurrence, resulting in low syntopy among hybridizing species that do not also engage in interspecific territoriality. (C) Under the misdirected aggression and the resource competition hypotheses, interspecific territoriality should primarily be found between species that encounter each other infrequently (low syntopy) or between species with similar ecological niches and breeding habitats (high syntopy). The resource competition hypothesis further predicts a negative relationship between niche overlap and syntopy among non-interspecifically territorial species. (D) Under the misdirected aggression and asymmetric competition hypotheses, interspecific territoriality occurs between species that either are high in syntopy, with one species dominating aggressive interactions, or that are low in syntopy.

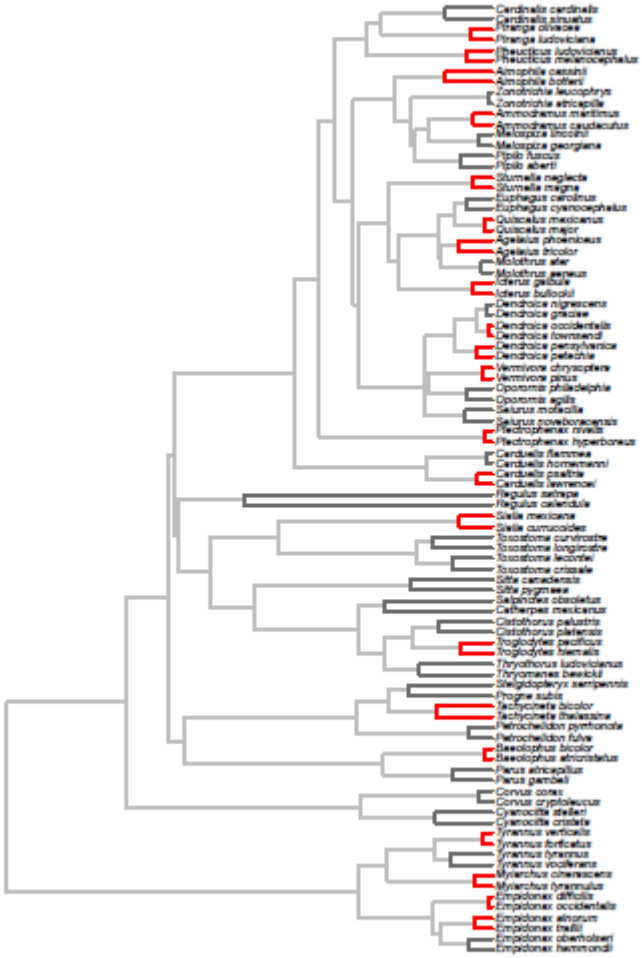


Figure 2. Interspecifically territorial sister species (red) are separated by shorter patristic distances (shaded branches; Ma), on average, than non-interspecifically territorial sister species (dark gray).

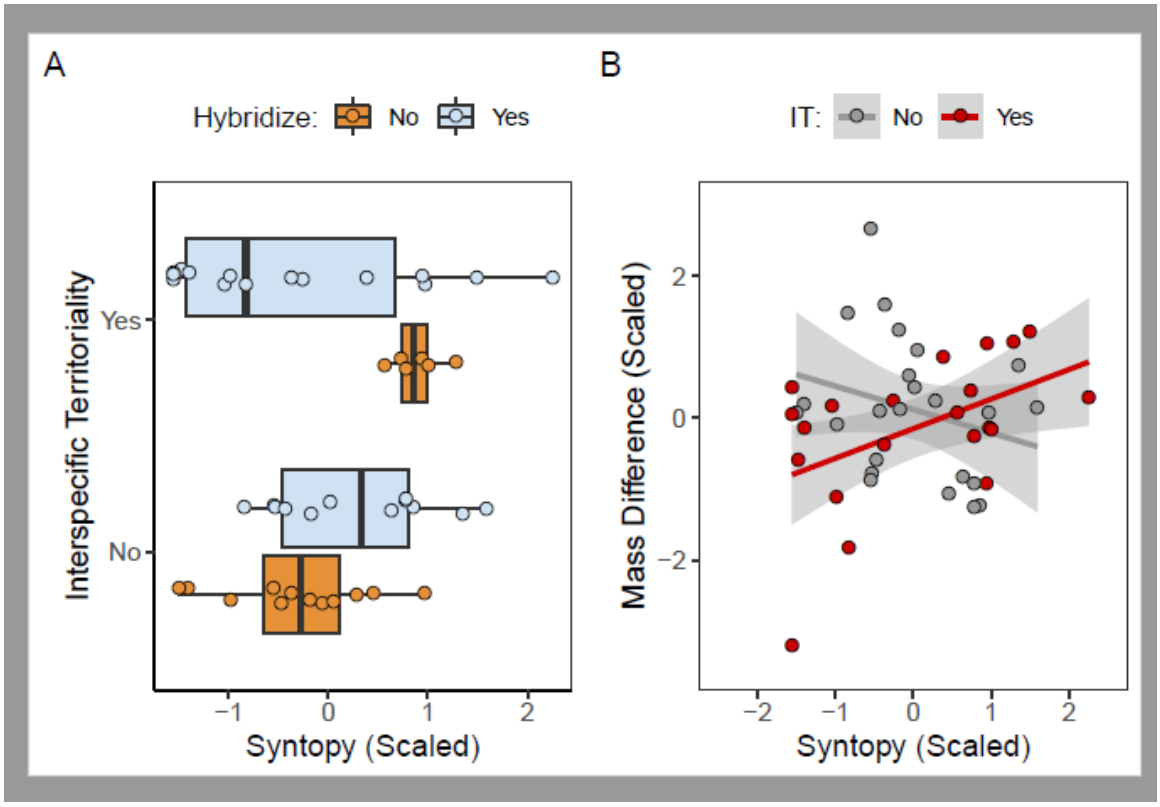

Figure 3. Interaction plots showing that (A) interspecifically territorial species that hybridize are less syntopic than non-interspecifically territorial species that hybridize, while interspecifically territorial species that do not hybridize are more syntopic than non-interspecifically territorial species that do not hybridize; (B) interspecifically territorial species (red) are more similar in size when low in syntopy than when high in syntopy, while the reverse is true for non-interspecifically territorial species (gray). Shading represents 95% confidence intervals. Mass difference and syntopy are both scaled to have a mean of zero and standard deviation of 1.

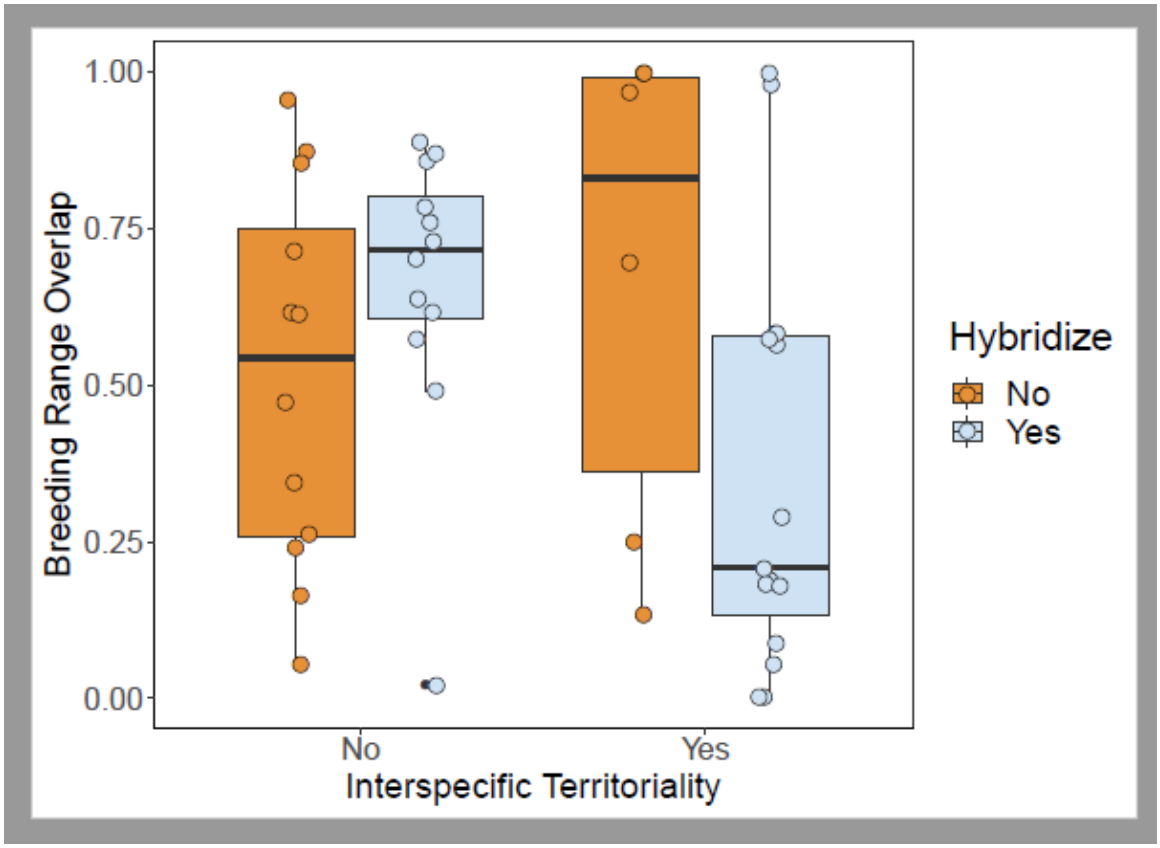


Figure 4. Interaction plot depicting the relationship between breeding range overlap and the interaction between interspecific territoriality and hybridization (also see Table S11).

**Table 1. Direction of association[†] between predictor variables and interspecific territoriality, as predicted by four hypotheses.**

| | Misdirected aggression | Adaptive for resource competition | Adaptive for reproductive interference | Adaptive for asymmetric competition |
|---|---|---|---|---|
| Patristic distance | – | – | – | – |
| Plumage dissimilarity | – | – | – | |
| Song similarity | + | + | + | |
| Foraging guild overlap | | + | | + |
| Bill length difference | | – | | – |

| | | | | |
|---|---|---|---|---|
| Mass difference | | – | | + |
| Hybridization | + | | + | |
| Syntopy | – | + | + | + |

†+, positive association; –, negative association

**Table 2. Univariate comparisons between interspecifically territorial (I.T.) species pairs (N = 20) and non-interspecifically territorial (non-I.T.) species pairs (N = 25), and coefficients of variation.**

| | | Non-I.T. pairs | | I.T. pairs | | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | Transformation | Mean | SE | Mean | SE | t | $P_{t\text{-test}}$ | CV |
| Patristic distance | log | 2.10 | 0.04 | 1.44 | 0.04 | 2.35 | **0.012** | 117.86 |
| Song similarity (SPCC) | | 0.34 | 0.01 | 0.40 | 0.01 | -1.61 | 0.058 | 35.68 |
| Song dissimilarity (PCA) | | 5.77 | 0.08 | 4.91 | 0.09 | 1.53 | 0.067 | 35.33 |
| Mass difference | log(x + 0.01) | 1.16 | 0.07 | 0.69 | 0.08 | 0.89 | 0.189 | 332.87 |
| Plumage dissimilarity | | 1.76 | 0.04 | 1.78 | 0.04 | -0.09 | 0.535 | 49.85 |
| Syntopy | log(x + 0.01) | -3.59 | 0.02 | -3.57 | 0.04 | -0.09 | 0.536 | 95.49 |
| | | Median | Range | Median | Range | | $P_{Mann\text{-}Whitney}$ | CV |
| Bill difference | log(x + 0.01) | 0.28 | -4.61 – 2.94 | -0.09 | -4.61 – 1.51 | | 0.120 | 159.06 |
| Sympatry | sqrt | 0.79 | 0.14 – 0.98 | 0.54 | 0.05 - 1 | | 0.093 | 61.93 |

**Table 3. Generalized linear model predicting interspecific territoriality with interaction between syntopy and hybridization.**

| Variable | Estimate | SE | *z* | *P* |
|---|---|---|---|---|
| (Intercept) | -3.31 | 2.38 | -1.39 | 0.165 |
| Syntopy | 5.60 | 2.81 | 2.00 | **0.046** |
| Hybridization | 3.72 | 2.08 | 1.79 | 0.074 |
| Plumage dissimilarity | 0.36 | 0.43 | 0.83 | 0.409 |
| Song dissimilarity (PCA) | -0.32 | 0.50 | -0.63 | 0.526 |
| Song similarity (SPCC) | -0.23 | 0.55 | -0.42 | 0.676 |
| Mass difference | -0.15 | 0.41 | -0.37 | 0.71 |
| Bill length difference | -0.02 | 0.44 | -0.04 | 0.965 |
| Guild overlap | -0.19 | 1.23 | -0.15 | 0.878 |
| Syntopy x hybridization | -6.17 | 2.85 | -2.16 | **0.031** |

**Table 4. Generalized linear model predicting interspecific territoriality with interaction between syntopy and mass difference.**

| Variable | Estimate | SE | *z* | *P* |
|---|---|---|---|---|
| (Intercept) | -0.27 | 0.91 | -0.29 | 0.769 |
| Syntopy | -0.02 | 0.39 | -0.06 | 0.956 |
| Mass difference | -0.15 | 0.57 | -0.27 | 0.791 |
| Guild overlap | -0.64 | 1.06 | -0.60 | 0.546 |

| | | | | |
|---|---|---|---|---|
| Hybridization | 0.79 | 0.86 | 0.92 | 0.359 |
| Plumage dissimilarity | 0.41 | 0.42 | 0.97 | 0.33 |
| Song dissimilarity (PCA) | -0.42 | 0.39 | -1.08 | 0.278 |
| similarity (SPCC) | 0.17 | 0.50 | 0.33 | 0.74 |
| Bill length difference | 0.06 | 0.50 | 0.12 | 0.907 |
| Syntopy x mass difference | 1.80 | 0.75 | 2.41 | **0.016** |

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